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The richness of small pockets: decapod species peak in small seagrass patches where fish predators are absent

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Abstract

Patchy landscapes behave differently from continuous ones. Patch size can influence species behaviour, movement, feeding and predation rates, with flow-on consequences for the diversity of species that inhabit these patches. To understand the importance of patchiness on regional species pools, we measured decapod richness and abundance in several seagrass patches with contrasting sizes. Additionally, we evaluated potential drivers of patch-specific species distribution including resource abundance, predator habitat use and the structural complexity of patches. Our results showed a non-random distribution of decapod species: small patches were clear hotspots of diversity and abundance, particularly of larger-bodied epifaunal decapods. Interestingly, these hotspots were characterized by lower nutrient resources, lower canopy height, but also lower predator use. Small fish invertivores such as *Coris julis* and several species of *Symphodus* were mostly restricted to large patches. These resident predators may be critical in clumping predation in large patches with consequences for how biodiversity of their prey is distributed across the seascape. Our results highlight the idea that a habitat mosaic with both large and small seagrass patches would potentially bolster biodiversity because preys and predators may seek refuge in patches of different sizes.

Keywords: Biodiversity, Fish use, Top down control, Mediterranean Sea, Patch size, species richness, *Posidonia oceanica,* predation

1. Introduction

Vegetated seascapes are often spatially heterogeneous, typically occurring as mosaics of vegetated patches surrounded by a matrix of sand that separates each patch from other vegetated areas. Patchy landscapes behave very differently from continuous ones. Patch size can influence species recruitment, behaviour, movement, feeding and predation rates, with flow-on consequence for the diversity of species that inhabit these patches (Andren 1992, Williams 1964; Connor & MacCoy 1979, Pittman 2011). Unsurprisingly then, in patchy interconnected landscapes, patch size has been one of the principal metrics used to predict local and regional species abundance and distribution. Basic island biogeography principles applied to these patches suggests that the number of species at a location could be predicted by patch size and isolation merely by considering immigration and extinction probabilities, with larger patches typically accumulating a higher species richness (MacArthur and Wilson, 1967). However, island biogeography predictions cannot easily be ported to landscape and seascape scales, where other factors likely play vital roles in determining assemblage patterns. Patches may not always behave like islands. For one, populations in patches are more connected through individual dispersal from adjacent patches than are populations between islands (Menendez & Thomas 2000). This connectivity is often species specific, with life history traits fundamental in determining species-area relationship outcomes. Small isolated patches will likely affect the survival of habitat specialists with limited dispersal abilities much more than vagile generalist, for whom a fragmented landscape may be perceived as sufficiently connected (Thomas 2000). Additionally, most benthic species, even those with low mobility, have planktonic phases of dispersal, for which habitat fragmentation may not typically determine settlement (Gaines et al. 2007; Robertson and Butler Iv 2009). Finally, where spatial heterogeneity interacts with ecosystem processes (i.e. predatory-prey interactions, competition), the distribution of vagile fauna can be determined at small scales (Boström, Jackson & Simenstad 2006). Landscape configurations can therefore drive a potentially predictable clumping of trophic processes (hot and cold predation spots, Nelson & Boots, 2008; Temming, Floeter, & Eherich, 2007).

Seagrass habitats range from large contiguous meadows to highly patchy seascapes. In the latter, multiple seagrass patches are embedded in a matrix (e.g. sediment) that affects animal movement and survival depending on habitat size and relative isolation (Tanner 2006, McNeill & Fairweather 1993, Bell et al. 2001, Orth et al. 2006). This spatial heterogeneity can be the result of natural or anthropogenic fragmentation or colonization processes (Gera et al. 2014, Tamburello et al. 2012), and can strongly influence the diversity of flora and fauna within the seascape (Bell *et al.* 2001; Hovel 2003; Arponen & Boström 2012). This is particularly true for species associated with seagrass leaves and rhizomes, many of which are highly site attached

(Gacia *et al.* 2009, Manjón-Cabeza et al. 2009; Ramírez and García Raso 2012). Causes of local spatial patchiness include differential recruitment, differential access to food resources, active and passive dispersal or differential growth and mortality. Recruitment may be patch size dependent with medium sizes having more recruits than small and large patches (Reusch 1998). This patch dependency has also been observed in growth rates of filter-feeding bivalves for which less vegetation and smaller patches may be more beneficial (Carroll & Peterson 2013). Patch configuration can influence the way resources are distributed in the seascape. Small patches capture or retain less detrital material, making them relatively poorer in nutrient availability (Ricart et al 2015) and potentially affecting plant growth and habitat structure (see Gera et al 2013). Predator-prey interactions, acting at local scales, can also drive heterogeneous diversity patterns (Boström et al. 2011), for instance when the distinctive distributions of predatory fish within fragmented meadows cause variations in predation impact (Fernández et al. 2005). In highly mobile predator species, predation hotspots result in a non-random distribution of their prey in patchy seascapes (Farina et al. 2017). This has also been observed in fish herbivores, where landscape attributes determine the non-random distribution of herbivores (Pagès et al. 2014). However, this predation distribution is not always consistently linked to patch size within the meadows. Highly fragmented seascapes may not provide adequate shelters and the relationships between predation intensity and vegetation cover may not always be linear (Böstrom et al. 2011). Other factors such as the within-patch composition and location of the patch on the shore can also influence the effect of the patch size (Mills & Berkenbusch 2009).

What is clear is that understanding how marine organisms respond to seagrass seascape configurations is complex, the result of several drivers acting simultaneously, and at different spatial scales. If predation is the main driver, we should expect prey distribution to be linked to predator abundance that in turn may be related to landscape attributes (Farina et al. 2017). However, if other factors such as differences in resource availability or competition are the main drivers, patch size may be critical in determining species distribution, with diversity and abundance increasing with patch size. Our objective in this study was to understand how the patchiness of a seascape influences the regional species pool of decapods. We estimated decapod richness and abundance associated with the leaves of patches of contrasting sizes in highly heterogeneous seagrass meadows. Additionally, we evaluated potential drivers of patch-specific species distribution including resource abundance, predator habitat use and the structural complexity of patches.

2. Materials and Methods

2.1. Study design and sampling site

We assessed the species richness and abundance of decapods in seagrass canopies in small (≤ $3m^2$) and large (> $10m^2$) randomly chosen seagrass patches (n=6 of each). Patches were selected on a ~15km stretch of the Western Mediterranean dominated by highly heterogeneous meadows (41°41' N, 002°50' E, Gera et al. 2013). All of our selected patches were embedded in a sandy matrix separated by at least 2 m from other patches (average distance between patches ~5m), to ensure a similar degree of isolation. At each of the patches we additionally measured seagrass nutrient content (resource abundance), predatory fish habitat use and canopy height (structural complexity).

2.2. Decapod abundance and diversity

We sampled canopy-dwelling decapod diversity and abundance in *P. oceanica* patches in summer using a towed hand net sampling method. The device consisted of a rectangular frame (40x20cm), with a 50 cm long handle, with a net (mesh size 250 μm) long enough to prevent the escape of fauna caught in its folds (130cm) and a small plastic jar attached to its end (Russo 1985). We marked off a 1x1 meter quadrat for each sample, sampling the seagrass canopy with 30 constant strokes of the hand net per quadrat (see Russo et al. 1985 for details of the sampling technique). We sampled a total of 36 quadrats (3 replicates per patch, 6 patches per size, 2 sizes). To avoid variability caused by potential edge effects, all samples were situated along the patch edge since the small patches were too small to sample their centre.

2.3. Fish patch use

We measured fish habitat use to estimate the presence of potential decapod predatory fish in the patches. We sampled the same small and large patches from which decapods were sampled (see above). We additionally sampled two more patches per size class since we expected larger variability in fish habitat use (n=8 patches per size, a total of 16 samples). We set GoPro (Full HD) cameras in patches attached to an iron bar at a fixed distance (60cm) from the edge of the patch (see Boada 2015 for details). We recorded videos for 30 min in each patch (the first and last 5 min were discarded to avoid SCUBA divers' effect, effective video duration = 20 min). For each video we calculated fish patch use of the most common and abundant associated predatory fish species (i.e. *Coris julis, Symphodus spp, Diplodus spp*, Bell & Harmelin-Vivien 1983, Guidetti 2000). Fish use of habitats was expressed as the percentage of time a given fish species was present in a patch. We calculated the percentage of time spent by each fish species in a given patch by adding the number of individuals of each species for the time they were present within the patch (in minutes), and then dividing it by the total video sampling time (20 minutes). The overall time of predatory fish use was obtained by adding the time of all fish species together related to the total time video sampling time (20 min). In addition, although our

136 sampling was not designed for larger-ranging shoaling species, we checked all videos to
137 quantify any *Sarpa salpa* (the predominant herbivore fish in these waters, Prado et al 2007)
138 recorded.

139 *2.4. Seagrass nutrient content*

140 Most species of decapods we recorded were mesograzers (feeding on epiphytes) and deposit
141 feeders (Gambi et al. 1992). To evaluate potential competitive exclusion related to nutrient
142 limitation (resource quality) in different patch sizes, we measured the nutrient content (nitrogen)
143 in *P. oceanica* rhizomes. This is a highly reliable and integrative method to detect differences in
144 nutrient availability in the water and the environment (see Roca et al 2015 for more details). We
145 collected two seagrass shoots per patch. The top 2 cm of rhizome were separated, dried at 70ºC
146 for 48 hours and ground to a fine powder and pooled to obtain an adequate amount of sample
147 for subsequent analysis. Rhizome nitrogen concentration was measured using an Elemental
148 Analyzer FlashEA1112 (ThermoFinnigan Unidade de Técnicas Instrumentais de Análise,
149 Universidade de Coruña). Two of the patches, one for each treatment were not found at the end
150 of the experiment and only 5 patches were sampled for this variable. However, given the low
151 variability of this measurement we are confident that if there were differences in this variable
152 due to patch size they would be detected despite the lower sample size (see Gera et al. 2013).

153 *2.5. Seagrass structure*

154 We evaluated differences in habitat structure between patch size as a potential driver of species
155 richness and abundance by measuring canopy height at each of the patches. We did this at the
156 same time as our other sampling to ensure there were no seasonal changes. The length of *P.*
157 *oceanica* leaves influences the degree to which the habitat offers prey species chances to hide
158 from predators (Farina et al. 2009, Pagès et al 2012). We estimated canopy height (cm) in the
159 patches sampled for decapod fauna by measuring the vertical distance between the substrate and
160 the top of the standing leaves in two different randomly selected areas within each patch. Since
161 we could not find one patch of each treatment (see above) only 5 patches were sampled for this
162 variable (2 replicates, 5 patches, 2 size classes).

163 *2.5. Statistical Analysis*

164 To determine the effects of patch-size on the dependent variables 'decapod species richness'
165 and 'decapod species abundance' we performed general linear models with a Poisson
166 distribution and the explanatory variable 'Patch Size': 2 levels small ($\leq 3m^2$) and large ($>10m^2$)
167 and patch (3 replicates per patch) as a random factor. A negative binomial distribution was used
168 to deal with over-dispersion when necessary (i.e. for 'total decapod abundance'). Similarly, we

used generalized linear models with either Poisson or Gaussian distributions (as required) to assess the effect of 'Patch Size' to the three different processes analysed; i) fish habitat use, ii) nutrient resources and iii) canopy height. Patch was included as a random factor in the nutrient resources and canopy height model. All the statistical analyses were performed in R using *lme4* package for the general linear model analyses (R Development Core Team 2013, Bates et al. 2016).

3. Results

3.1. Decapod diversity

Decapod species richness and abundances were significantly higher in small patches. The average number of total individuals per patch was 39±5 individuals/m^2 for small patches, while the abundance in large patches was 28±3 individuals/m^2 (Fig. 1b, Table 1). Similarly, small patches hosted a significantly greater species richness with an average of 2.9±0.5 species/m^2 compared to 1.3±0.1 species/m^2 in large patches (Fig. 1a, Table 1). The most common and abundant species (*Hippolyte prideauxiana*) was ubiquitously distributed regardless of patch size (Fig. 1c). In contrast, other species were mainly present in the small patches (i.e. *Cestopagurus timidus, Hippolyte garciarasoi* and *Thoralus cranchii,* Fig. 1d,e,f). Additionally, the three largest decapod species were only present in the small patches, despite being relatively scarce in general (i.e. carapace length: *Macropodia rostrata* 7.0-7.5mm, *Pisa tetraodon* 11.5-12.2mm, *Pisa nodipes* 12.5-12.7mm, Table 2).

3.2. Fish patch use

The overall predatory fish use of patches was greater in large patches. The average use of large patches by predatory guilds was ~49.1±5.5 %, compared to 27.4±4.8 % in small patches (Fig. 2b, Table 3). This trend resulted from the high % use of large patches by *Coris julis* and by species of the genus *Symphodus* (see Fig 3a, b). However, species from the genus *Diplodus*, which are known to be very territorial and display restricted home ranges (<1km^2) (Aspillaga et al. 2016), appeared to use both patch sizes similarly (Fig. 3c). No shoals of the herbivorous fish *Sarpa salpa* were recorded in the videos. However, video recording might not be the best technique to determine the abundance of shoaling fish species, with relatively large home ranges (Pagès et al. 2013).

3.3. Seagrass nutrient content

We found nutrient content to be higher in larger patches with average values of ~1.75±0.2%N compared to small patches in which the %N was ~1.07±0.2 (Fig. 2a, Table 3).

201 *3.4. Habitat structure*

202 Finally, we also found differences in canopy height between patches of different sizes (Fig. 2c,
203 Table 3). Large patches had, in general, higher canopy height with an average of 30.6±2cm long
204 leaves compared to smaller patches, where leaves were 22.9±2cm long, on average (Fig. 2c).

205

206 **4. Discussion**

207 Our results show a clear non-random distribution of decapods with patch size across the
208 *Posidonia oceanica* seagrass seascape. We found large patches to be less rich in decapod
209 species and with lower abundances. Thus, small patches appear to be hotspots of decapod
210 diversity and abundance. Of the various hypotheses that could potentially explain how patch
211 size influences species richness and abundance, our observations point strongly to the role of
212 top-down control. As expected from previous studies in the same system (Gera et al 2013,
213 Ricart et al 2015), larger patches had more resources (i.e. nitrogen content in seagrass leaves,
214 detrital material) and were structurally more complex (i.e. taller canopies), factors typically
215 linked to enhanced diversity and abundance. However, these large patches had several resident
216 fish predators. Predators were much less frequent in small patches, making them refuges of
217 decapod diversity and abundance. In addition, the largest species of decapods, which were more
218 susceptible to mobile predatory fish, were only present in the small patches. Overall, our results
219 highlight the potential effect of predation in shaping decapod distribution.

220 Small patches have their limitations. Refuge, resources retention and nutrients are often
221 limiting (Gera et al 2013, Ricart et al 2015), and as species scramble to appropriate them,
222 competitive exclusion should likely leave smaller patches with fewer species (Murray and Baird
223 2008; Keymer et al. 2012). As resources decline, competitive exclusion alone can predictably
224 explain the local extinction of species in smaller, putatively less nutritious and unprofitable
225 patches (Kolb 2008). For a range of groups, from infaunal macroinvertebrates, decapods and
226 fish, studies have shown a positive species-area relationship (Bowden et al. 2001, Boström et al.
227 2006). Similarly, nutrient limitation or physical degradation of small patches caused by habitat
228 fragmentation can seriously impact the survival of non-mobile fauna due to changes in food
229 availability and increased predation risk (Villafuerte et al. 1997). The prevailing assumption
230 then is that decreasing patch sizes should result in lower species diversity of decapods
231 communities (Reed et al 1982, Birkely & Gulliksen 2003). Surprisingly, our results showed the
232 opposite trend, with a clear peak of decapod diversity and abundance in small, less structured
233 *Posidonia oceanica* patches. Earlier studies on seagrass systems have documented similar
234 results, showing that the density of faunal groups (decapods, fish, bivalves) either do not

respond or increased with reducing patch size, linked to positive edge effects (area/perimeter relationship, Hirst and Attrill 2008; Arponen and Boström 2012). Although we did not record herbivores in our video samples, herbivory on small patches could certainly interact with lower nutrients to reduce overall canopy heights (Gera et al 2013). Our study does not test if increased light availability in lower-canopied small patches could increase decapod diversity and abundance, by favouring epiphyte growth. Given that some species of decapods are consumers of the epiphyte community (Gambi et al. 1992), this potential feedback cannot be ruled out and is an avenue for further studies.

The uneven distribution of diversity across a patchy seascape can be generated and strengthened by predator-prey interactions responding to local-scale ecosystem processes (Boström et al. 2011). In our study, predatory fish showed a clear preference for large patches; thus, predation pressure clearly increased with increasing habitat size. In a similar study Hovel and Fonseca (2005) show that smaller seagrass patches served as predation refugia for blue crabs. This has also been observed in mobile insects that actively select larger patches to forage, ignoring smaller patches (Lienert 2002, Haynes and Crist 2009). Since the ability to perceive habitats is determined by the size, vision and movement characteristics of an animal, the effects of patch size on predatory fish behaviour can be highly relevant (Macreadie et al. 2009). This was also proposed by Eggleston et al. (1999) as an explanation for higher predation on grass shrimp (*Palaemonetes spp*.) and small, mobile crustaceans (i.e. amphipods and isopods, but not of *Hippolytes* spp shrimps) in artificial seagrass habitats with different patch sizes. Additionally, Micheli and Peterson (1999) found that medium sized predators may avoid moving into fragmented areas of an habitat, since they have limited refuge and are potentially more vulnerable to larger predators (also supported by Morales-Nin and Moranta 1997; Moranta et al. 2006). The most abundant fish groups recorded in our study had distinct preferences for larger patches, which are also potentially the best refuges. Small fish invertivores such as *Coris julis* and several species of *Symphodus* that are important decapod consumers (Bell and Harmelin-vivien 1983) were mostly restricted to large patches where they could potentially find better refuge from their own predators. The exceptions were species from the genus *Diplodu*s that we found using small and large patches equally. This genus comprises several, very different generalist species and are typically not seagrass-specific (i.e. *Diplodus sargus*, *Diplodus vulgaris*, *Diplodus annularis*). Resident predators may be critical in maintaining hotspots of predation in large patches with consequences for all larger species of leaf-associated decapods that were absent.

Predator behaviour can have major implications for diversity patterns across landscapes (Lima and Zollner 1996) . If landscape attributes modify that behaviour, changes in landscape

can result in a very different distribution of species across space. Disentangling the relationship between predator behaviour, landscape attributes and diversity patterns is essential to understanding how processes like fragmentation are likely to affect ecosystem functioning, particularly in strongly top-down controlled ecosystems (Lima and Zollner, 1996). For seagrass meadows, seascape configurations can drive a potentially predictable clumping of medium size fish predators in large patches that in turn can drive decapod leaf-associated species to concentrate in small patches. These resident predators may be critical in maintaining hotspots of predation in large patches with consequences for how biodiversity of their prey is distributed across the seascape. Seagrass seascapes with a matrix of small and large patches may potentially bolster biodiversity because preys and predators may seek or find refuge in patches of different sizes.

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Table 1. Mean values and SE for decapod species richness and abundance in large and small patches. P-values show the results from generalized linear models testing the effect of patch size (fixed factor) on decapod species richness and abundance (response variables). Patch number was included as random factor. Significant p-values are given in bold.

Patch Size	Species richness	SE	Total Abundance	SE
Large	1.28	0.11	28.28	2.91
Small	2.89	0.49	39.67	5.05
P value	**<0.01**		**<0.03**	

Table 2. Mean abundance value ± standard error per patch size for each species. Carapace length in mm of each species is also given.

Site	Large patches	Small patches	Size Range (mm)
Hippolyte prideauxiana	27.8±2.9	28.7±3.8	1.6-4.2
Cestopagurus timidus	0.4±0.2	2.2±1.1	1.5-2.4
Macropodia rostrata	0	0.3±0.1	7.0-7.5
Palaemon xiphias	0	1.1±0.4	4.6-11.3
Hippolyte garciarasoi	0	3.7±2.7	1.5-3.5
Pisa nodipes	0	0.1±0.1	12.5-12.7
Thoralus cranchii	0	3±1.4	2.0-3.6
Pisa tetraodon	0	0.2±0.1	11.5-12.2
Eualus occultus	0	0.3±0.3	1.8-3.2
Galathea bolivari	0	0.6±0.6	3.5

Table 3. Results from generalized linear model testing the effect of patch size (fixed factor) on nutrients, fish habitat use and habitat structure (response variables; processes). Patch number was used as a random factor in models for nutrients and structure. A Poisson distribution was used in model for fish use.

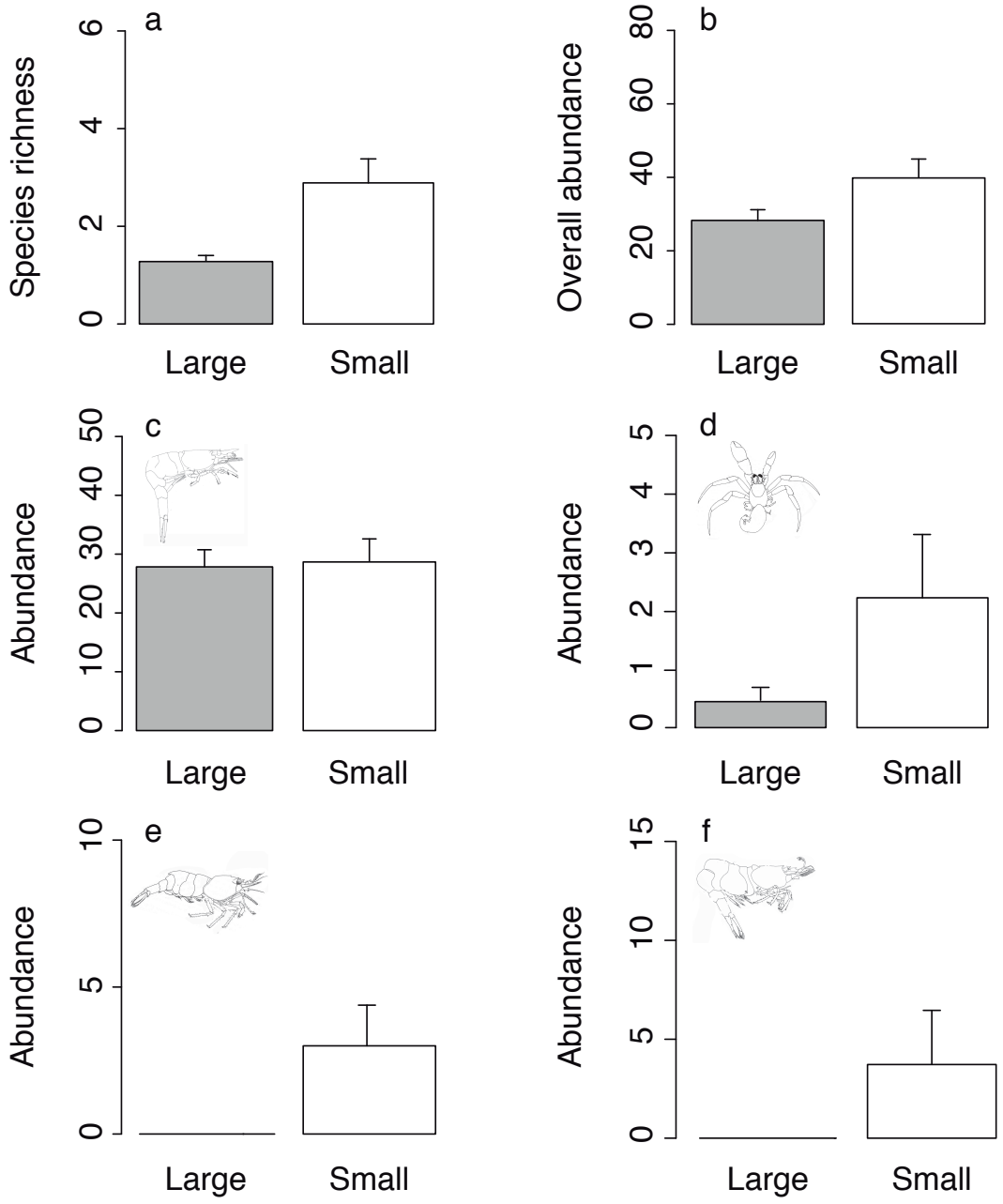
Response	DF	Chi Sq	P value	Factor
Nutrients	1	5.44	**0.02**	Patch size
Fish use	1	10.626	**<0.01**	Patch size
Structure	1	6.98	**<0.01**	Patch size

Figure 1. Decapod species richness and abundance (individuals per square meter) in large (filled) and small (blank) seagrass patches. a) mean number of species ± standard error (SE) found in samplings (18 for large and 18 for small patches). b) mean number of individuals of all the species pooled found in samplings ± SE. The rest of the plots represent the mean abundance ± SE found for each of the species c) *Hippolyte prideauxiana*, d) *Cestopagurus timidus*, e) *Thoralus cranchii* and f) *Hippolyte garciarasoi* respectively.

Figure 2. Functional processes studied; resource limitation a) as percentage of nutrient content in plant tissues, fish use of the landscape b) as percentage use of patches by the fish predatory guild and the structural complexity of the habitat c) as canopy height (leaves length).

Figure 3. Fish habitat use of the landscape according to patch sizes. Filled grey bars represent the mean percentage use of the large patches ± SE (see methods) while empty bars represent the percentage use of small patches ± SE by predatory fish species, a) *Coris julis*, b) *Symphodus spp*, c) *Diplodus spp.*

530 **Fig. 1.**
531



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533 **Fig. 2.**

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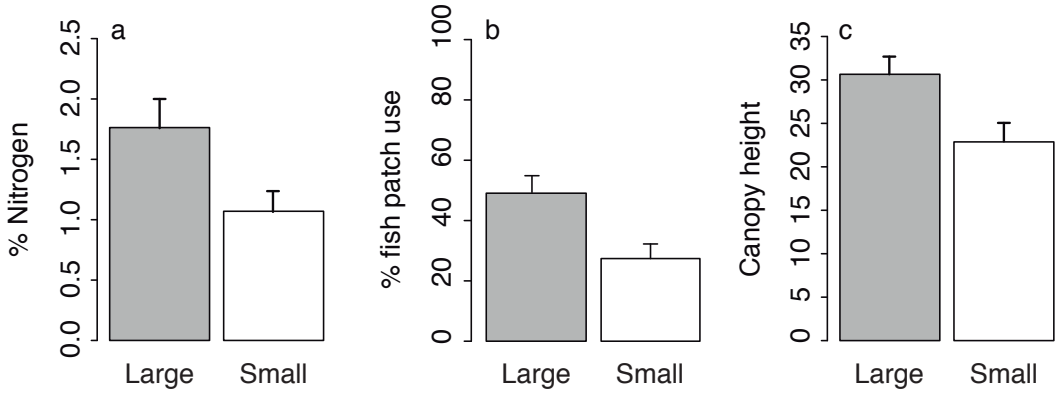

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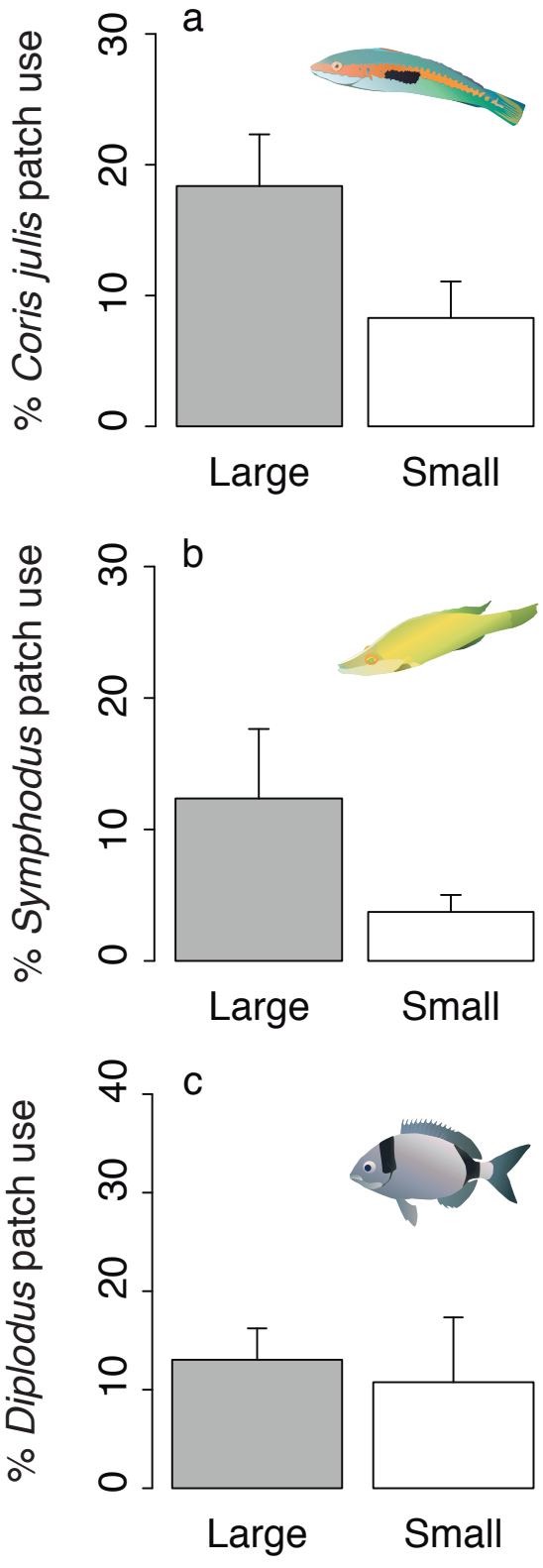
Fig. 3.


a
% Coris julis patch use
0
10
20
30
Large
Small
b
% Symphodus patch use
0
10
20
30
Large
Small
c
% Diplodus patch use
0
10
20
30
40
Large
Small